Trends of Specialization in the Stipe Anatomy of Dennstaedtia and Related Genera

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The scope and position of the dennstaedtioid ferns in the Filicales has varied considerably in systematic treatments. In Bower's (1926, p. 268, 1928, p. 5) system they were included in the Dicksoniaceae in a scheme which separated that family from the Cyatheaceae. Conard (1908) believed that *Dennstaedtia* belonged in the Polypodiaceae, as it was separable from the Cyatheaceae on characters of the annulus, antheridium, and prothallium. Separation of the tree ferns into Cyatheaceae and Dicksoniaceae was maintained by Holttum (1949). He placed the Dennstaedtiaceae in a central position as a large, complex family including 81 genera. Holttum's Dennstaedtioideae was considered the most primitive of 11 subfamilies. Later Holttum and Sen (1961) demonstrated a close relationship between *Cyathea, Dicksonia, Culcita* and *Cibotium* on the basis of the development of the sorus. This removed the main objection to uniting the tree ferns into one family, but *Dennstaedtia* was regarded as belonging to a different group of genera, even though there is evidence of some relationship with the tree ferns. Holttum and Sen (1961) did not attempt to answer whether the above genera should be considered as belonging to subfamilies of a single family or remain as separate families, but Holttum (1963, pp. 71–72) placed them in three subfamilies of the Cyatheaceae.

The stipe anatomy of the dennstaedtioid (including pteroid) and cyatheoid ferns shows greater structural complexity than that of any other extant group of ferns. While some of these stipes have been described in the past (Gwynne-Vaughan, 1901, 1903, p. 721; Bertrand and Cornaille, 1902, p. 47; Conard, 1908; Bower, 1926, p. 264, 1928, p. 5; Holttum and Sen, 1961; Tryon, 1962),

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[1] I wish to express my appreciation to the Organization for Tropical Studies, San José, Costa Rica, for providing financial support and facilities for the conduct of this investigation. Also I am grateful to Drs. W. H. Wagner, Jr., J. T. Mickel, E. de la Sota, D. B. Lellinger, and A. M. Evans for their advice and encouragement.

the characteristics of stipe anatomy have not been utilized comprehensively in taxonomy. The present survey was undertaken to establish the degree of variability and the trends of specialization of this feature. I believe that taxonomically important characters are present.

TABLE I. VOUCHERS AND CHARACTER STATE CHANGES IN DENNSTAEDTIOID AND PTEROID FERNS.

Species	*Voucher number*	*Specialization*[1]
Blotiella lindeniana (Hook.) Tryon	3432	2, 4, 5, 7
Dennstaedtia arborescens (Willd.) Ekman ex Maxon	3111	4
D. bipinnata (Cav.) Maxon	2697, 3505	3, 4, 5
D. cicutaria (Swartz) Moore	3118	1, 4
D. dissecta (Swartz) Moore	2946	3, 4, 5
D. obtusifolia (Willd.) Moore	2947	1, 3, 4
D. spinosa Mickel	2730	4
Histiopteris incisa (Thunb.) J. Smith	3193	2, 7
Hypolepis bogotensis H. B. K.	3248	1, 2, 4, 5
H. pulcherrima Underw. & Maxon	3306	3, 4, 5, 6
H. repens (L.) Presl	2743	2, 4
H. sp.	*s.n.*	2, 4
H. sp.	3428	1, 4, 5
Lonchitis hirsuta L.	2590	2, 3, 4, 5, 7
Loxsomopsis costaricensis Christ	3001	3, 4, 5
Paesia anfractuosa (Christ) C. Chr.	3000	1, 2
Pteridium aquilinum (L.) Kuhn	*s.n.*	1, 2, 4, 5
Pteris altissima Poir. in Lam.	*s.n.*	–
P. podophylla Swartz	3279	2, 4, 5
P. pungens Willd.	3563	3, 4, 5
Saccoloma elegans Kaulf.	2799	1, 5
Saccoloma inaequale (Kunze) Mett.	2755	1, 5

[1] Numbers are of those characters from *Table III* which show the advanced state.

During July and August, 1967, I examined 17 genera and 33 species of ferns in Costa Rica (*Tables I* and *II*). Where vouchers were collected, the collection numbers of John T. Mickel are given. Specimens have been deposited at US. The anatomy of nearly all of the species was checked several times; in no case were there significant variations from the patterns drawn from the cited specimens. Freehand thin sections of stipe bases were prepared from fresh specimens and were examined and drawn under 50× magnification with a dissecting microscope. Particular attention was paid to the anatomy of the vascular trace and to the course of the xylem. Sections made throughout the length of the stipe of many specimens indicated that no fundamental changes take place distally; only a reduction in size occurs as the pinnae are vascularized. To assure uniformity of comparison, all cross sections illustrated are from stipe bases. For several representative genera, preserved material was used to prepare stained microtome sections to confirm details of histology.

TABLE II. VOUCHERS AND CHARACTER STATE CHANGES IN CYATHEOID FERNS.

Species	*Voucher number*	*Specialization*[1]
Alsophila spp.	2795, 3291	1, 2
Culcita coniifolia (Hook.) Maxon	3238	1, 4, 5
Cyathea aureonitens Christ	2948	1, 2
C. maxonii Underw.	*s.n.*	1, 2
Dicksonia gigantea Karst.	3134	1, 2, 3, 6
Hemitelia choricarpa Maxon	2797	1, 2
H. costaricensis (Kl.) Mett. ex Kuhn	2861	1, 2
Lophosoria quadripinnata (Gmel.) C. Chr.	3638	1, 2, 4, 6
Metaxya rostrata (H. B. K.) Presl	2853	1, 3

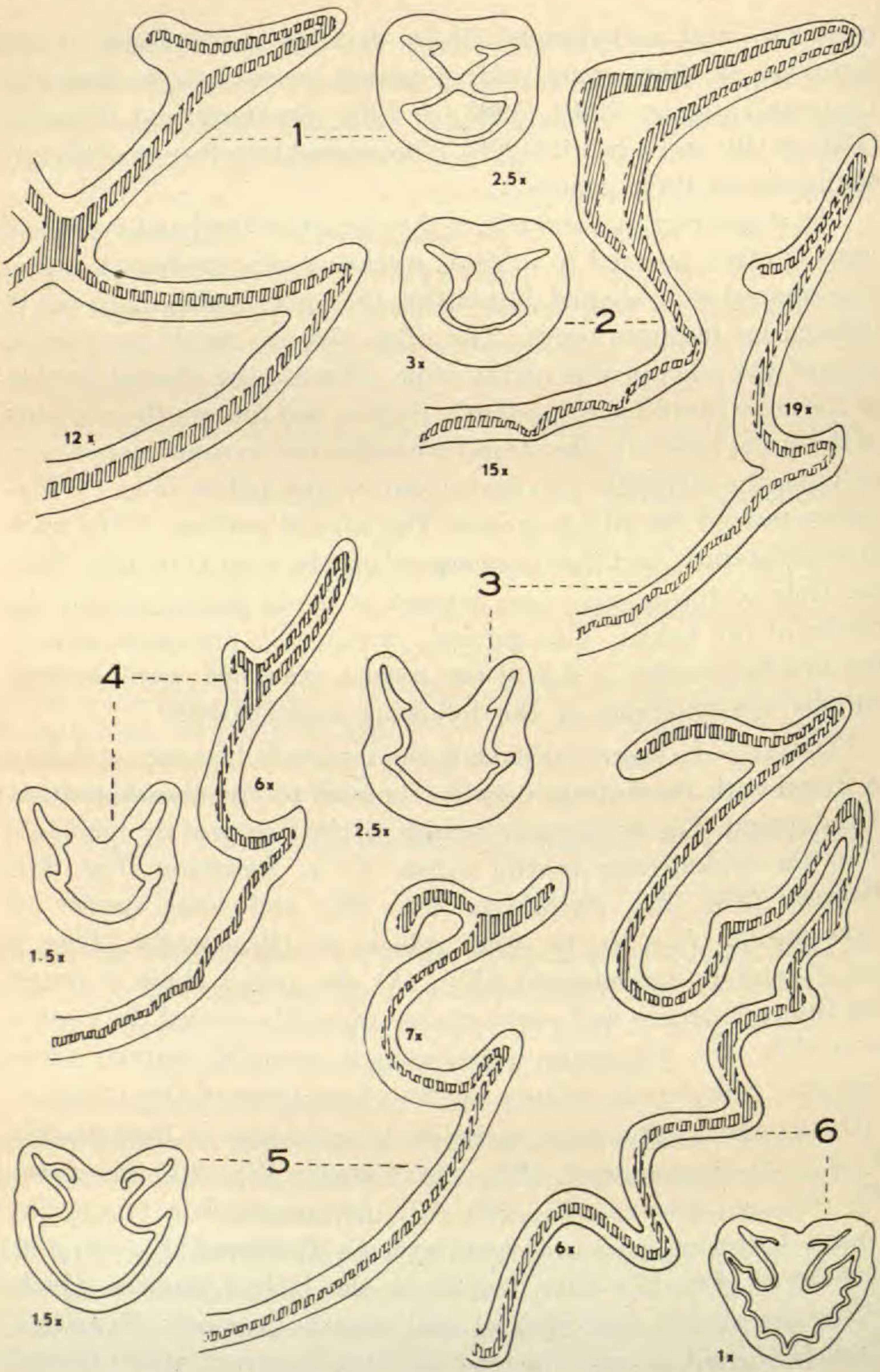
[1] Numbers are of those characters from *Table III* which show the advanced state.

Nearly all of the genera in this investigation have a single adaxial groove on the stipe and rachis. On all specimens the abaxial portion is uniformly convex in outline. The stipes are either convex or slightly grooved laterally. An aeration line is often present in the lateral groove or above it. The stipes contain one or more meristeles each completely surrounded by an endodermis. At the center of the meristele is the xylem, which is one to several cells thick and which is surrounded by layers of parenchyma, phloem, pericycle, and endodermis. More detailed descriptions of the histology of solenosteles and of petiole traces can be found in Gwynne-Vaughan (1901, 1903, p. 726), Bertrand and Cornaille (1902, p. 49) and Conard (1908). The general histology is strikingly similar in all these genera.

The stipe trace or meristele of the dennstaedtioid and cyatheoid ferns is often referred to in cross section as omega-shaped, horseshoe-shaped or U-shaped, but within this general plan a number of differential features occur. The open side of the U is oriented toward the adaxial side of the stipe, whereas the abaxial portion of the stipe strand is consistently convex and follows the contours of the stipe. Laterally the strand is constricted, in some cases nearly dividing the meristele into dorsal and ventral halves (*Fig. 1*). This can be termed the lateral groove. The adaxial portions of the trace diverge laterally and then converge along the adaxial margin. Here the ends of the U may turn inward as hooks facing toward the center of the rachis. This general, presumably primitive, plan is not totally present in any of the species examined; each exhibits various combinations of the following modifications:

FLUTING.—In many specimens the meristele becomes undulate or fluted with the flutings usually confined to the abaxial portion of the strand. The fluting may include all the tissues of the meristele from the endodermis to the xylem, as in *Dicksonia* (*Fig. 25*), *Metaxya* (*Fig. 23*), *Saccoloma* (*Fig. 20*), and some species of *Dennstaedtia* (*Fig. 6*). In other species of *Dennstaedtia* (*Figs. 2* and *3*) and in *Loxsomopsis* (*Fig. 18*) the xylem alone is fluted and the endodermis and pericycle are smoothly curved. In *Lophosoria* (*Fig. 21*), the outer endodermis is smoothly curved while the inner endodermis follows the fluted contours of the xylem.

DISSECTION.—The stipe meristele is unbroken in *Dennstaedtia* (*Figs. 1–6*), *Loxsomopsis* (*Fig. 18*), *Culcita* (*Fig. 19*), *Saccoloma* (*Fig. 20*), and *Metaxya* (*Fig. 23*). All other genera show tendencies toward dissection in at least some species. *Dicksonia* (*Fig. 25*) and *Lophosoria* (*Fig. 21*) have breaks in the lateral grooves which divide the strand into adaxial and abaxial portions. *Hypolepis* (*Figs. 8, 11*, and *13*) and *Paesia* (*Fig. 9*) have breaks at the lateral



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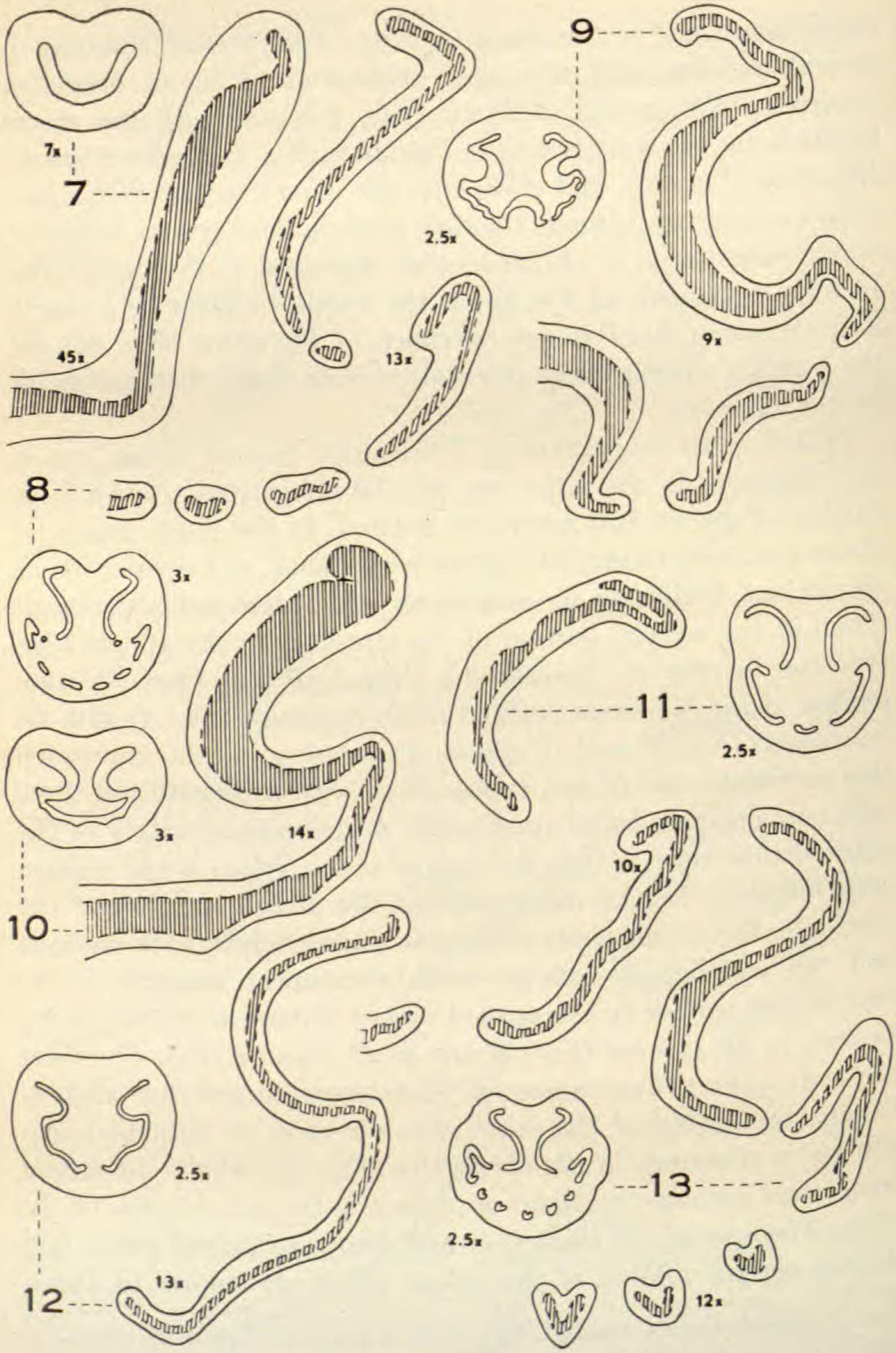
invagination and in the abaxial portion of the strand, resulting in several bundles with the same orientation as in an unbroken meristele. One species of *Pteris* (*Fig. 16*) examined also shows breaks in the abaxial portion. In *Pteridium* (*Fig. 24*) and in *Cyathea, Hemitelia* (*Fig. 26*), and *Alsophila*, the stipe vasculature consists almost exclusively of small bundles. Even in these genera, however, bundle orientation is similar to that described as the basic form. In some specimens of *Pteridium* the bundles appear as a nearly formless mass. Only in one specimen of *Pteridium* (*Fig. 24*) did the bundles show a clear orientation with easily distinguishable lateral grooves.

FUSION AND REDUCTION.—Tendencies toward stelar fusion and reduction in the stipe can only be interpreted when a large number of species and genera are studied. In this study nearly all of the various intermediate stages were found, and several trends are evident. Reduction in complexity of the stele and in the orientation of the adaxial portion of the strand from the ground plan type can be seen in *Dennstaedtia*, *Hypolepis* and *Pteris*. A comparison of the meristele outlines of *D. bipinnata* (*Fig. 2*) with *D. arborescens* (*Fig. 5*) and *D. cicutaria* (*Fig. 6*) gives the impression that meristeles are of two types: those with divergent and those with convergent adaxial trace ends. A closer examination of the figure details reveals that the course of the xylem is the same in each instance. In the outer edge of the adaxial portion of the meristele, the xylem tends to become folded tightly back on itself and the endodermis follows more economical contours (i. e., exposes less surface to the ground tissue). Intermediate stages can be seen in *D. spinosa* (*Fig. 1*) and in *D. dissecta* (*Fig. 3*), where the end of the xylem causes the endodermis to protrude slightly toward the center of the stipe. The direction of reduction tendencies is obscured in *D. obtusifolia* (*Fig. 4*), where the xylem completely encloses an island of phloem in the adaxial ends of the stele. The species of *Hypolepis* and *Pteris* examined show tendencies toward folding of the xylem which are similar to *Denn-*

FIG. 1. DENNSTAEDTIA SPINOSA. FIG. 2. D. BIPINNATA. FIG. 3. D. DISSECTA. FIG. 4. D. OBTUSIFOLIA. FIG. 5. D. ARBORESCENS. FIG. 6. D. CICUTARIA.



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staedtia. In the abaxial portion of the meristele, just below the lateral groove, a trend toward the folding of the xylem within the stele occurs in *Dennstaedtia* (*Figs. 3–5*) and in *Hypolepis* (*Figs. 8, 10*, and *11*).

LATERAL GROOVE DEPTH AND POSITION.—Constriction of the strand shows much variation. In *Cyathea, Alsophila*, and to some extent in *Hemitelia* (*Fig. 26*) the lateral groove is deep and narrow, dividing the stipe vasculature nearly equally in half between adaxial and abaxial portions. In *Hypolepis* (*Figs. 8, 10, 11*, and *13*) and *Dennstaedtia* (*Figs. 1–6*) the groove is oriented toward the adaxial side of the meristele and is variously shallow or deep. In *D. spinosa* (*Fig. 1*) the grooves are deep enough to allow the meristele to connect at the center of the stipe. The deeper grooves are found in larger stipes with generally more complex vasculature. Shallow grooves are due partly to general decrease in size and partly to previously mentioned folding and fusion tendencies. In *Pteris altissima* (*Fig. 15*) the grooves reach the extreme in orientation toward the adaxial side. In *Dicksonia* (*Fig. 25*) the grooves are located in the most abaxial position of any genus in this study.

CONCLUSIONS

It is difficult to conceive that independent origins are possible for genera with such similarity of ground plan in stipe anatomy. There is no reason to expect that features of stipe anatomy are sufficient in themselves to allow construction of a phylogeny (Bailey, 1951), but some trends of specialization are evident. In *Table III* the character states of stipe anatomy are presented as observed in this study. These trends are not based on solid evidence of unidirectional sequences, but on the fact that species with putatively reduced stipe features seem specialized in other characters. The conclusions of Bertrand and Cornaille (1902, pp. 40, 98, 211)

FIG. 7. HYPOLEPIS PULCHERRIMA. FIG. 8. H. SP. FIG. 9. PAESIA ANFRACTUOSA. FIG. 10. HYPOLEPIS SP. FIG. 11. H. BOGOTENSIS. FIG. 12. BLOTIELLA LINDENIANA. FIG. 13. HYPOLEPIS REPENS.

and Gwynne-Vaughan (1901, p. 95) regarding reduction and dissection were also used in establishing the directions of specialization.

None of the data have produced any straight line sequences of related genera. It is apparent, however, that similar evolutionary specializations have occurred. There seem to have been two major lines of specialization: the dennstaedtioid line and the cyatheoid line.

TABLE III. CHARACTER STATES IN STIPE VASCULATURE.

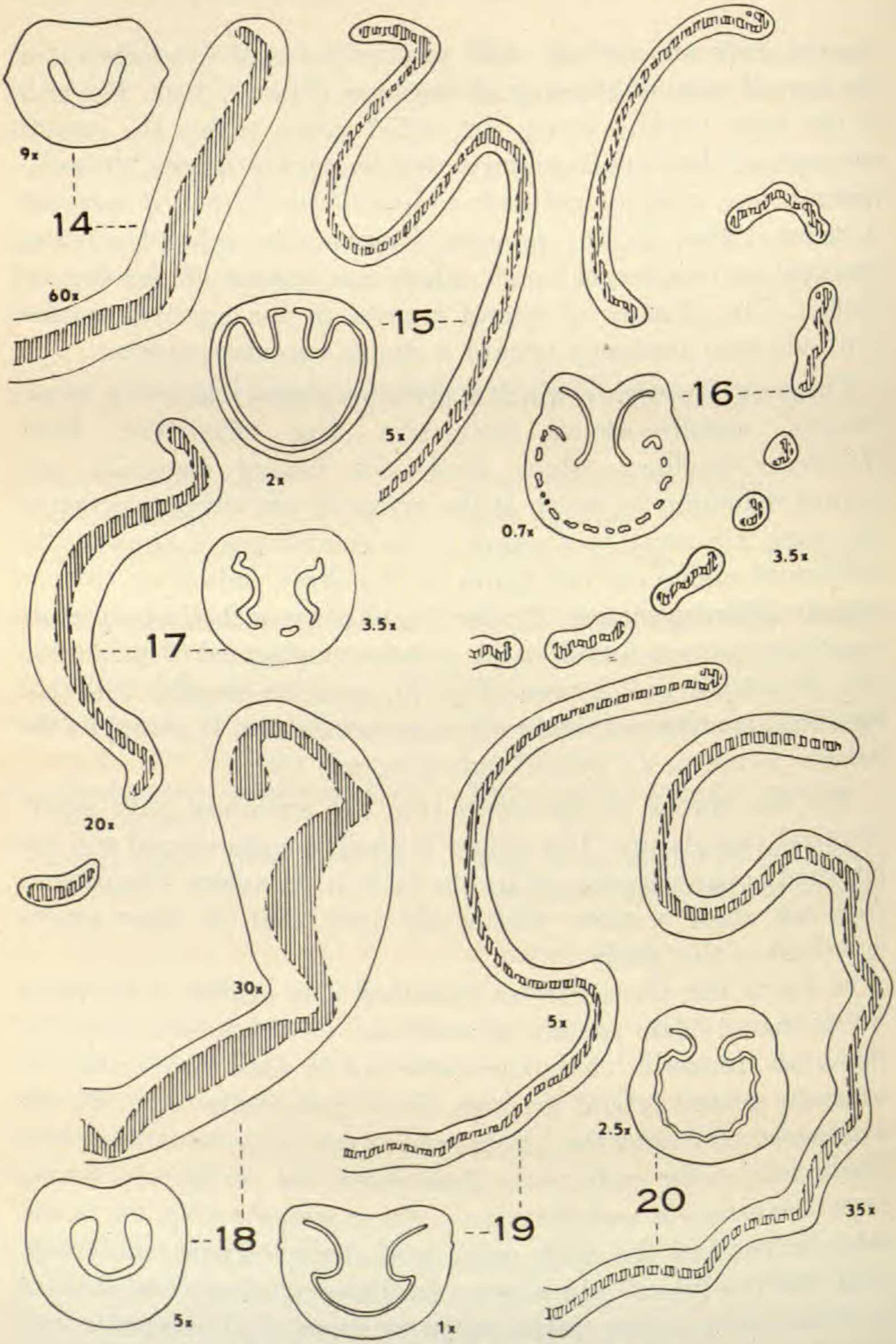
Primitive	*Advanced*
1. Stele contours smooth.	Contours fluted or undulate.
2. Stele unbroken.	Stele dissected.
3. Deep lateral grooves.	Shallow grooves or "U"-shaped trace.
4. Xylem symmetrically disposed between the outer and inner endodermis of the meristele.	Xylem fluted or folded within smooth contoured meristele margins.
5. Adaxial ends of the trace convergent and hooked.	Trace ends divergent or simple with erect ends.
6. Lateral groove centrally or adaxially oriented.	Lateral groove abaxially oriented.
7. Abaxial portion of the trace continuous.	Break in or absence of the abaxial portion of the trace, the vasculature divided into two equal lateral halves.

Table I lists specimens of dennstaedtioids with the character numbers from *Table III* which show the advanced state. In *Dennstaedtia* several trends are evident rather than a straight line of evolution. All the species of *Dennstaedtia* show at least one change from the generalized condition. The most consistent trend has been toward the elimination of the convergent ends of the trace on the adaxial side. This has occurred by the gradual folding of the inturned portion and hooks so that they lie flat against the sides of the stele, which tends to form a trace with U-shaped ends. In many species the remnants of the convergent ends are seen as small protrusions in the endodermis of the inward sides of the ends of the trace (*Figs. 1, 3, 4*). The ends of the trace usually reveal the folded xylem within the smooth contours of the stipe boundary. One temperate species, *D. punctilobula,* has a highly reduced, simple, V- or U-shaped meristele (Conard, 1908). Within the stele, however, the xylem has lateral grooves and convergent ends which are typical of the tropical species. The absence of lateral grooves in the meristele outline is a reduction tendency toward a simple vascular pattern.

The genus *Hypolepis,* which is probably a close relative of *Dennstaedtia,* usually shows distinctive stipe characters. Some *Hypolepis* specimens show tendencies toward dissection and toward reduction in length of the xylem on the abaxial portion of the trace. The small protrusions in the endodermis of *Dennstaedtia* mentioned above are not found in *Hypolepis,* indicating either a slightly different pattern of reduction or perhaps that intermediate conditions are not found in the species investigated (*Figs. 11* and *13*). *Hypolepis pulcherrima* (*Fig. 7*), with its simple, U-shaped meristele, has the most reduced stipe vasculature. It resembles the pattern found in *D. punctilobula* (Conard, 1908).

The two species of *Saccoloma* (*Fig. 20*) examined have nearly identical vasculature. The strand is nearly omega-shaped and the inturned hooks are gone, as are the folds in the xylem. The pattern does not show a close relationship with that of other genera described in this study.

In *Pteris* the three species examined also exhibit a divergent rather than a linear pattern of evolution. *Pteris altissima* (*Fig. 15*) shows no change in character states but is distinctive in having adaxially placed lateral grooves. *Pteris podophylla* (*Fig. 16*) has a dissected stele and the adaxial convergent ends have been lost. The xylem at the ends of the stele shows the vestige of a fusion as in *Dennstaedtia* and *Hypolepis. Pteris pungens* (*Fig. 14*) is the most reduced of the three, with a U-shaped strand with erect ends and the loss of lateral grooves. The evolutionary tendencies in *Pteris* show a clear relationship to those of *Dennstaedtia* and *Hypolepis.*



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Histiopteris incisa (*Fig. 17*) shows a distinct resemblance to *Hypolepis*. Its further specialization involves the loss of much of the abaxial portion of the trace which, in further reduction in *Blotiella* and *Lonchitis*, leaves two lateral traces instead of a U. *Blotiella lindeniana* (*Fig. 12*) is reminiscent of the *Pteris* type, but is also similar to *Paesia anfractuosa* (*Fig. 9*) with its abaxial deformation of the stele. It is also suggestive of *Hypolepis*, as pointed out by Tryon (1962). *Lonchitis hirsuta* (*Fig. 22*) possesses two traces oriented as in the thelypterid ferns; it is conceivable that the latter group is derived by this kind of reduction from the basic dennstaedtioid type. The vasculature of some species of *Thelypteris* and *Diplazium* resembles the dennstaedtioid type to a striking degree (Alan R. Smith, pers. comm.).

Pteridium aquilinum (*Fig. 24*) is a specialized type without direct relationship with other genera. The stipe stele is completely dissected, and tends toward apparent disorganization into a mass of bundles. The outline of the bundles includes an abaxial deformation which resembles the pattern of *Paesia* (*Fig. 9*) rather closely. On the basis of the features exhibited by these specimens, these genera might well be associated with the *Hypolepis-Histiopteris* line.

The cyatheoid ferns have been suggested by Holttum and Sen (1961) to belong to a separate line of evolution. Their changes in character states are listed in *Table II*. The cyatheoids have undergone as divergent an evolution as has *Dennstaedtia* and its immediate relatives. Although *Culcita* (*Fig. 19*) is associated with *Dicksonia* (*Fig. 25*) on the basis of other evidence, the divergent ends of the stipe stele with folded xylem (*Fig. 19*) is reminiscent of *Pteris*, *Dennstaedtia*, and *Hypolepis*. *Culcita dubia*, however, is reported to have inflexed ends on the stele (Holttum and Sen, 1961), and so the genus is probably compatible with *Dicksonia*. All other members of this assemblage of genera have well-developed vasculature with convergent adaxial ends with inward pointing hooks. *Lophosoria* (*Fig. 21*) and *Dicksonia* show close similarities,

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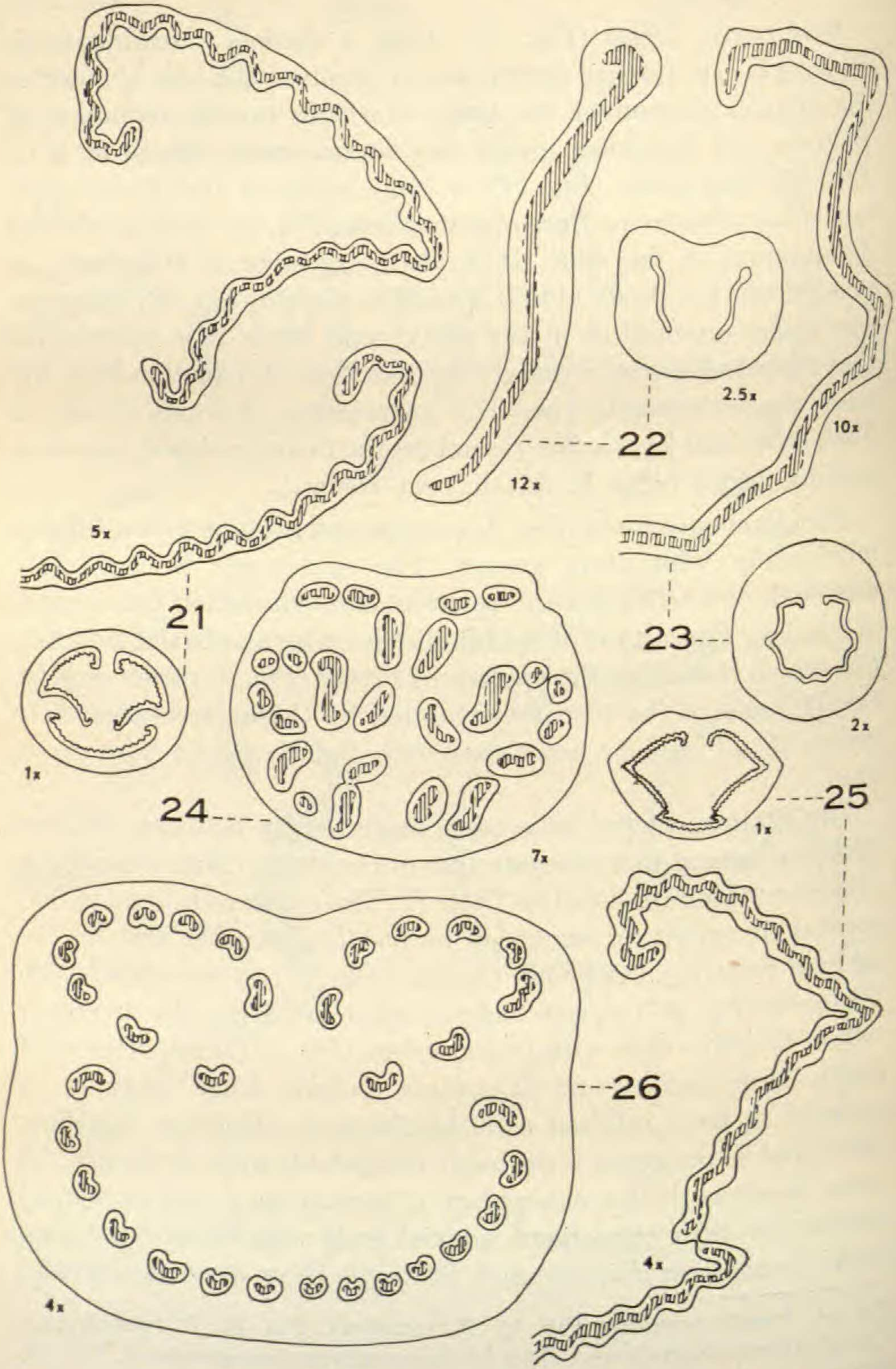
FIG. 14. PTERIS PUNGENS. FIG. 15. P. ALTISSIMA. FIG. 16. P. PODOPHYLLA. FIG. 17. HISTIOPTERIS INCISA. FIG. 18. LOXSOMOPSIS COSTARICENSIS. FIG. 19. CULCITA CONIIFOLIA. FIG. 20. SACCOLOMA ELEGANS.



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and *Metaxya* (*Fig. 23*) shows the same general plan. *Alsophila, Hemitelia* (*Fig. 26*), and *Cyathea* have stipes with the same basic configuration as *Lophosoria* except that dissection has taken place.

The conclusions of Holttum and Sen (1961) are supported in this investigation. The cyatheoid and dennstaedtioid lines of descent seem to be divergent lines from a common ancestor. In the cyatheoids the differences in dissection of the stipe trace support the suggestion by Maxon (1911) that the Cyatheaceae be divided into the Cyatheae and Dicksonieae. While it is probable that the cyatheoids terminate an evolutionary line, it is quite likely that the dennstaedtioids have given rise to other groups. The basic ground plan of the stipe in the dennstaedtioids is not incompatible with that found in many unrelated groups of ferns. Specimens I observed which show similarities in stipe vasculature include species of *Asplenium, Blechnum, Cheilanthes, Gleichenia, Jamesonia, Lindsaea, Odontosoria, Phlebodium, Polypodium, Thelypteris, Trichomanes,* and *Trismeria*. Although the stipes of each of these genera show diagnostic differences and, on the basis of stipe anatomy, no close relationship between them should be postulated, in each a high degree of simplification from the presumably primitive type is shown. Some have vestiges of lateral invaginations and convergent ends in the xylem even though the vasculature may consist of a simple arc of meristeles As noted by Gwynne-Vaughan (1901, p. 95), this apparently universal design seems, with some exceptions, to be fundamentally typical for the Filicales. One could argue that parallel evolution could produce this ground plan in unrelated groups of ferns. The evidence from stipe anatomy for the species illustrated would not support any suggestion that these genera are polyphyletic. Different combinations of a limited number of modifications suggest radiation from a common ancestor. Available data promises that an extensive survey of the stipe anatomy in the Filicales would contribute greatly to our knowledge of phylogeny within that order.

FIG. 21. LOPHOSORIA QUADRIPINNATA. FIG. 22. LONCHITIS HIRSUTA. FIG. 23. METAXYA ROSTRATA. FIG. 24. PTERIDIUM AQUILINUM. FIG. 25. DICKSONIA GIGANTEA. FIG. 26. HEMITELIA CHORICARPA.

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Shorter Notes

A NOTE ON ASPIDOTIS.—The late E. B. Copeland was the first among modern pteridologists to take up *Aspidotis* (Nutt. ex Hook. & Bak.) Copel. as a genus. This genus is a segregate of *Cheilanthes*, although it was originally described as a section of *Hypolepis* and was considered a subgenus of that genus by Christensen. The New World species are distinguished by elongate, narrow, generally mucronate-rostrate and distantly toothed segments with thickened margins and a striate and shining upper surface and with broad, scarious, continuous or discontinuous